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Group sizes of giraffes in Kenya: the influence of habitat, predation and the age and sex of individuals

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Abstract

Giraffe group sizes appear to vary in response to localised ecological and environmental factors, but there has been little investigation of how social factors or predation risk affect group size in giraffes. We studied two adjacent, enclosed populations of Rothschild's giraffes in Kenya, and used 591 records of groups to determine the relative influence of a series of variables on group size. One population was free from any risk of predation, while the other area contained a high density of lions. Mean group size was smaller in the population with lions, but a series of GLMMs accounting for habitat and age/sex class of individuals showed that the presence of high numbers of juveniles in the area free from lions artificially inflated group sizes. Removing juveniles from the analysis showed that contrary to the existing creche hypothesis, adult females were found in smaller groups when they had calves. We found no evidence that predation risk influenced grouping behaviour. Rather, recruitment and habitat type had a stronger influence on group sizes, but the results were complex and varied between different age and sex classes of individual. We conclude that predation is not an important driver of giraffe grouping, and that further research is necessary to understand the complex behaviour and ecology of this prominent yet understudied species.

Keywords: *Giraffa camelopardalis*, Rothschild's giraffe, group size, lions, predation, population demography, recruitment

Introduction

Temporal and spatial variation in animal groups arises as individuals balance the costs and benefits of group living to maximise fitness (Rodman, 1981; Krause & Ruxton, 2002; Thaker *et al*., 2010). By living in groups animals gain protection from predators, knowledge about the location of resources and access to mating opportunities, although these benefits must be traded off against costs such as increased competition for resources, aggression and risk of disease (Hamilton, 1964; Pulliam, 1973; Krause & Ruxton, 2002; Beauchamp, 2003). The grouping behaviour of a species is often modified by the additive effects of environmental and social factors (Price & Stoinski, 2007; White, Proffitt & Lemke, 2012; Creel, Schuette & Christianson, 2014), and fission-fusion societies are especially adept at altering their group sizes when conditions change (Estevez, Andersen & Nævdal, 2007). Such behavioural and group-level plasticity enables fission-fusion species to respond rapidly to changes in local conditions, and achieve an optimal balance between the costs and benefits of grouping (Aureli *et al*., 2008).

Protection from predators is one of the most frequently cited benefits of grouping, and predation has a strong and multifarious influence on the lives of prey species. As well as the direct risk of being predated, the presence of predators can reduce reproductive success and affect the population growth of prey species (Werner *et al*., 1983; Zanette *et al*., 2011; Creel *et al*., 2014). Reduced reproduction rates as a consequence of perceived predation risk (Zanette *et al*., 2011) may occur due to animals altering the time they invest in vigilance and foraging behaviours (Brown & Kotler, 2004) or by changing patterns of habitat use, which influences their ability to forage successfully (Sih & McCarthy, 2002; Creel *et al*., 2014). The presence of predators typically elicits increased vigilance and grouping behaviour (Krause & Ruxton, 2002; Creel & Winnie, 2005; Creel *et al*., 2014) but the strength and consistency of these responses varies between species (Creel *et al*., 2014). Increasing group size with increasing predation risk is reported across a variety of taxa (Crook & Gartlan, 1966; Seghers, 1974; Clutton-Brock & Harvey, 1977; Wrona & Dixon, 1991; Price & Stoinski, 2007).

Giraffes are an interesting species in which to study group living; early studies described giraffes as groups of random individuals with no long-lasting associations (Dagg & Foster, 1976; Leuthold, 1979; Le Pendu, Ciofolo & Gosser, 2000). However, new approaches and techniques have altered our understanding of their social structure and motivations for associating, and have identified linear hierarchies (Horová, Brandlová & Gloneková, 2015) and long-lasting preferred associations driven by kinship (Bercovitch & Berry, 2013a), home range overlap (VanderWaal *et al*., 2013), social preferences (Carter *et al*., 2013a) and age proximity (Bercovitch & Berry, 2013b; Carter *et al*., 2013b).

However, some of the most basic elements of giraffe ecology remain unknown. Variation in giraffe group sizes is believed to be a result of adaptive responses to local environmental and social conditions, such as habitat type and season (Ciofolo, 1995; Leuthold, 1979; van der Jeugd & Prins, 2000; Brand, 2007), sex of group members (Bercovitch & Berry, 2014) and the presence of predators (Creel *et al*., 2014). Lone individuals are common, mean group size is typically 3 to 9 individuals (Table 1). Groups are smaller in the presence of predators (Creel *et al*., 2014), suggesting that protection from predators is not a driver of grouping. Vigilance scanning increases as the number of males in a group increases (Cameron & du Toit, 2005), suggesting that there are reduced foraging costs for being in groups. It is generally accepted that females with calves congregate to form creche groups (Langman, 1977; Leuthold & Leuthold, 1978; Horwich *et al*., 1983; Pratt & Anderson, 1985), but this has never been explicitly tested. Fundamental questions about the adaptive advantages of grouping in giraffes are still unanswered.

In this study, we aim to further explore the hypothesis that giraffes group for predator-protection benefits. We also test the effects of habitat on group size, since giraffes should be more vulnerable in some habitats than others, which may affect grouping decisions. Lastly, we test the influence of the age/sex of individuals on grouping behaviour, since individuals of different age and sex class may have different strategies and motivations to form or disband from groups (Bercovitch & Berry, 2014).

Materials and Methods

Study sites and data collection

We collected group size data at two locations in the Great Rift Valley region of Kenya: Soysambu Conservancy (SC) is a 190km^2 wildlife conservancy surrounding part of Lake Elementeita (00°46'S, 036°23'E; 1670m asl), and Lake Nakuru National Park (LNNP) is a 188km^2 National Park surrounding Lake Nakuru (0°22'S 36°05'E; 1759m asl). Both areas are enclosed and separated by an electrified game-proof fence along the 7.8 km shared boundary along the south-eastern boundary of LNNP and western boundary of SC (Fig. 1).

The risk of predation is a notable difference between the two areas. Lions are the only predator to pose a significant threat to giraffes (Hirst, 1969; Pienaar, 1969; Foster & Dagg, 1972; Dagg & Foster, 1976; Strauss & Packer, 2013). In 2011, LNNP contained 56 lions (Ogutu *et al*., 2012), which is a high density (0.3 lion/km^2) compared to more typical densities of 0.08 and 0.14 lion/km^2 (East, 1984; Creel & Creel, 1997). Preferential preying of lions upon giraffes has been identified as a problem in LNNP (Kenya Wildlife Service, 2002; Brenneman *et al*., 2009). At the time of this study, SC was free of lions and had been for several decades (5th Baron Delamere, pers. comm.). This information is the basis of our assertion that giraffes in LNNP were exposed to a higher risk of predation than those in SC.

Data were collected for nine consecutive months in each study site (SC May 2010 to January 2011; LNNP May 2011 to January 2012), matched by time of year to reduce seasonal or climatic effects as far as possible. We searched for giraffe groups by driving a 4x4 vehicle at 20km/hr along pre-defined routes through each study site. Each route was driven in a randomised order and direction between

sunrise at 06:30 and sunset at 18:30 (UTC + 3h Standard Time), and the whole study site was searched each day.

A group of giraffes was defined as all individuals within 1km of each other and engaged in generally similar behaviour (Foster, 1966; Foster & Dagg, 1972; Leuthold, 1979; Le Pendu *et al*., 2000; Carter, 2013). Each group was observed for a minimum of 30 minutes, to ensure that all group members were seen and reliably identified.

Individual covariates: sex and age

In line with previous studies (Foster, 1966; Foster & Dagg, 1972; Pratt & Anderson, 1979, 1985; Young & Isbell, 1991; van der Jeugd & Prins, 2000; Le Pendu *et al*., 2000) we used four age classes: juvenile (<12 months), subadult (12 months to <4 years), adult (≥4 years) and big bulls (mature adult males with dark coats and skull nodules, ≥9 years old) (Pellew, 1984; Pratt & Anderson, 1985; van der Jeugd & Prins, 2000; Berry & Bercovitch, 2012). All giraffes were individually identified, sexed and verified: see Muller (2018) for complete methodology.

Habitat types

Habitat was classified into three categories: *Acacia* woodland, mixed woodland and open plain. *Acacia* woodland was any wooded area comprising ≥85% *Acacia* species. Mixed woodland was any wooded area comprising ≤85% *Acacia* species, and typically contained mixed tree and shrub species including *Euphorbia* spp*., Acacia* spp. and *Olea africana* (Mutangah, 1994). Open plain was any open savannah or grassland area.

Data Analysis

Records of group size were used in a one-way ANOVA to assess differences in mean group size, and in a Generalized Linear Mixed Model (GLMM) to determine which factors (population, age/sex class, habitat type, individual ID) affected group size across the two study populations. Population, age/sex class and habitat type were set as fixed effects. We accounted for the fact that individual giraffes could be seen in different groups by including 'giraffe (individual ID)' and 'group' as random effects to control for the non-independence of the group data. Since the group size distribution for each population was positively skewed (Fig. 2) we used a GLMM with a negative binomial error structure, which is appropriate for count data that are over-dispersed (Ridout *et al*., 1998; Gschlößl & Czado, 2008; Lindén & Mäntyniemi, 2011). The outcome of the GLMM was the group size in which an individual was found for a particular observation. Since individuals were observed repeatedly in different groups, individual was included as a random effect. An additional random effect for group was included since individuals within are not independent. All analyses were carried out in R 3.4.3 using the lme4 and gamlss.mx packages (R Development Core Team, 2013; Bates *et al*., 2014).

Results

There were 77 giraffes in SC (7 big bulls, 6 male adults, 12 male subadults, 16 female adults, 10 female subadults and 26 juveniles) and 89 giraffes in LNNP (11 big bulls, 19 male adults, 10 male subadults, 40 female adults, 4 female subadults and 5 juveniles); see Muller (2018) for discussion. We collected 591 records of group size: 298 groups in SC, 293 in LNNP. Group sizes were larger in SC (mean = 7.8, SD = 7.2, 95% CI 6.7, 9.1, min = 1, max = 37) than LNNP (mean = 5.3, SD = 5.5, 95% CI 4.7, 5.9, min = 1, max = 28). Lone individuals were common and accounted for 17.5% of all giraffe groups in SC and 24.7% in LNNP. Of these lone individuals, 84.9% and 76.6% were males in SC and LNNP respectively. Mean group sizes were not significantly different between habitat types within each population; SC: *Acacia* woodland = 11.6, mixed woodland = 6.2, open plain = 7.3 ($F(2, 47) = 2.432$, $p = 0.099$); LNNP: *Acacia* woodland = 4.8, mixed woodland = 4.9, open plain = 6.3 ($F(2, 309) =$

2.145, $p = 0.119$), but the proportion of groups observed in each habitat type differed between the two populations; in LNNP, 29% of groups were observed in *Acacia* woodland, 39% in Mixed woodland and 32% in open plain. In SC, 20% of groups were observed in *Acacia* woodland, 55% in mixed woodland and 25% in open plain.

A GLMM with population, habitat type and age/sex class as fixed effects and giraffe (individual ID) and group as random effects showed that the age/sex * habitat type * population interaction was significant (LRT chi-squared = 33.10, df = 20, $p = 0.0329$) (Fig. 3). We investigated the source of the interaction by analysing the effects of habitat type and population for each age/sex category separately (Table 2). There was no significant habitat * population interaction for adult males, bulls, adult females or juveniles. Group sizes tended to be highest in open plain (significantly higher than mixed woodland for all four of these age-sex categories), lowest in mixed woodland and intermediate in *Acacia* woodland.

For bulls, adult females and juveniles (but not adult males), group sizes were higher in SC than LNNP. For subadult males and subadult females there were significant Habitat * Population interactions. For subadult males, this was because group sizes were higher in SC than LNNP only for *Acacia* woodland; mixed woodland showed a non-significant trend in the same direction ($p = 0.0712$). For subadult females the pattern was more complex; groups sizes were significantly higher in SC than LNNP in *Acacia* woodland, but the reverse was true for mixed woodland.

Analysis without juveniles

To remove the artefacts of the presence of more juveniles *per se*, most notably in SC, driving up group size, we repeated the GLMM without including juveniles in the counts. The AgeSex * Habitat * Population interaction was significant (LRT = 31.66, d.f. = 16, $p = 0.0111$; Fig. 4), so we investigated the source of the interaction by analysing the effects of habitat type and population for each age/sex

179 category separately (Table 3). For adult males, bulls and adult females, there was no significant
180 Habitat * Population interaction, so we can readily interpret the main effects. Group sizes tend to be
181 highest in open plain (significantly higher than mixed woodland for all three of these age/sex
182 categories), with *Acacia* woodland intermediate. For bulls, but not adult males or females, group
183 sizes were higher in SC than LNNP. For subadult males and females there were significant Habitat *
184 Population interactions. For subadult males, this was because group sizes were higher in SC than
185 LNNP only for *Acacia* woodland. For subadult females, the pattern was more complex; group sizes
186 were significantly higher in SC than LNNP in *Acacia* woodland, but the reverse was true for mixed
187 woodland. Mean group sizes are displayed in Fig. 4.

188

189 *Analysis of groups sizes in females with and without calves*

190

191 To determine whether groups were bigger in SC due to the presence of more juveniles pushing up
192 mean group size, or if females were altering their behaviour because they had calves, we analysed
193 group sizes in females with and without calves. We refer to a female's status as having dependent
194 calves or not as Parity. The response variable was group size not including calves. The Parity x
195 Habitat * Population interaction was not significant (LRT = 0.70, d.f. = 2, p = 0.7034), so we then
196 tested the two way interactions. Of these, only Population * Habitat was significant (Population *
197 Parity: LRT = 0.26, d.f. = 1, p = 0.6121; Parity * Habitat: LRT = 2.59, d.f. = 2, p = 0.2745; Population *
198 Habitat: LRT = 13.49, d.f. = 2, p = 0.0012). The Population * Habitat interaction has already been
199 analysed so is not discussed further here. The main effect of Parity was also significant (LRT = 4.14,
200 d.f. = 1, p = 0.0417). Females with calves were found in smaller groups (by about 1 animal; Fig. 5),
201 but this did not interact with the habitat and population differences already identified.

202

Discussion

Knowledge of a species' behaviour and ecology is important for management and conservation (Sutherland, 1998) yet despite their prominence, giraffes are understudied in relation to other African mammals. Information about the social organisation of giraffes is confusing and contradictory, and factors influencing grouping behaviour are poorly understood. It is widely perceived that grouping behaviour in mammals is an anti-predator response, with most mammals exhibiting larger group sizes with increasing predation risk (Elgar, 1989; Wrona & Dixon, 1991; Krause & Ruxton, 2002). Our overarching hypothesis was that if predation is a driver of grouping behaviour in giraffes, then group sizes should be larger in the area with a high density of lions (LNNP). We set out to quantify the relative influence of habitat type, social factors and risk of predation risk on giraffe grouping behaviour.

Group size distribution was positively skewed in both populations with a high frequency of lone individuals, as in other studies (Foster & Dagg, 1972; Leuthold, 1979; van der Jeugd & Prins, 2000; Le Pendu *et al*., 2000; Bercovitch & Berry, 2010; VanderWaal *et al*., 2014). Lone individuals were more frequent in LNNP, probably due to the higher proportion of adult males (33% big bulls and adult males, vs. 17% in SC) which frequently roam alone (Foster & Dagg, 1972; Dagg & Foster, 1976; Bercovitch & Berry, 2014). Mean group size was smaller in LNNP, which is the opposite of what we expected, if predation was a driver of aggregations in giraffes. However, further analysis which accounted for habitat type, individual covariates and population, showed that the relationship between these variables and group size was complex.

To account for the effects of juveniles pushing up group sizes in SC, re-analysis after removal of juveniles confirmed that there was a significant influence of age/sex on group size. We found significant interactions between age/sex, habitat and population, but these patterns were also complex. Group sizes for males (adult males, subadult males and bulls; Fig. 4) were largest in the open plain habitat type, and generally smaller in LNNP. For females (adult and subadult), results

were mixed (Fig. 4). Our hypothesis that group sizes will be larger in the area with a high risk of predation was not supported, and our results highlight the complexity of factors contributing to group size in giraffes.

The hypothesis that females form larger groups when they have calves was not supported, and the opposite was true; females were found in smaller groups when they had calves. We found no evidence that increased mean group size in SC was due to females altering their behaviour to group with others when they had calves. Because the calves are counted as group members it seems most likely that the increased group size is solely because there are more calves, not because the females are joining together with other females to form creches. Although calves are typically found with their mothers, it appears unlikely that they contribute to their mother's decision to join or leave a group. Therefore, group sizes are not constrained by demography – rather, adults maintain their typical grouping patterns, but group sizes are smaller in LNNP due to the reduction in numbers of juveniles (Brenneman *et al*., 2009). Numerous sources in the literature describe how female giraffes form creche groups to care for their young (Langman, 1977; Leuthold & Leuthold, 1978; Horwich *et al*., 1983; Pratt & Anderson, 1985) and some evidence of alloparental care has been reported (Dagg & Foster, 1976; Pratt & Anderson, 1979; Gloneková, Brandlová & Pluháček, 2016). However, our results show that contrary to popular belief, females with calves are found in smaller groups than females without calves.

If giraffes gain predation protection benefits through grouping, then we would expect the group sizes to be larger in LNNP across all habitat types. However we found no evidence for this, and our results support previous studies which also reported smaller group sizes in the presence of predators (Creel *et al*., 2014), and that the rate of vigilance scanning in giraffes is not modified by changes in group size (Cameron & du Toit, 2005).

Our study is the first to examine two separate populations of giraffes within the same biome to attempt to understand the relative combined effects of predation, habitat and demographic factors

on grouping behaviour. We demonstrate that the presence of juveniles can artificially inflate group size results, and we suggest caution of over-interpretation of studies which do not account for this. We suggest that predator avoidance is not the main driver of giraffe grouping behaviour, but rather that social and habitat factors are likely to play an important role. We identify that removal of juveniles is potentially a problem in enclosed environments with high lion densities, which alters the greater social landscape for affected animal species. However, poor recruitment could also be due to other factors which cannot be ruled out, i.e. disturbance of foraging or reproductive activities by tourism, in-breeding factors, local environmental factors including food quality and availability, or differences in female fecundity, sexual receptivity, or harassment by bulls. The incongruous nature of group sizes of giraffes across Africa could be due to individuals adapting to local environmental conditions, but it is becoming clear that social factors are also important influencing variables. Variations could also be due to unknown taxonomic differences, given the uncertainty and ongoing debate over the taxonomic status of giraffes (Brown *et al*., 2007; Groves & Grubb, 2011; Bercovitch & Deacon, 2015; Fennessy *et al*., 2016; Bercovitch *et al*., 2017). We highlight the need for further research into this iconic species, and hope that our results contribute to the ongoing efforts to understand giraffe behaviour and ecology.

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435 **Table 1** Published reports of giraffe group size data. NR = Not reported. †Study looked at males only.
436 * Excludes group sizes of *n*=1.
437
438 **Table 2** Results from separate GLMMs on effect of Habitat (H) and Population (P) for each age/sex
439 category (AdM: adult male; SubM: subadult male; Bull; AdF: adult female; SubF: subadult female;
440 Juv: juvenile). If the Habitat * Population interaction was significant, the main effects are not
441 interpretable and, instead, separate GLMMs for the effect of Population are presented (as SC vs
442 LNNP) for each habitat type (MW: mixed woodland; AW: *Acacia* woodland; OP: open plain). Values
443 in each cell are likelihood ratio tests (p-values in italics). If the Habitat * Population interaction was
444 not significant, main effects of Habitat and Population are presented, and separate analyses of
445 Population differences for each Habitat are not applicable (na). Instead, where the main effect of
446 Habitat was significant, t-tests (and p-values in brackets) of pair-wise contrasts between habitats are
447 presented. The degrees of freedom for Habitat and the Habitat * Population interaction was 2; for
448 Population and pair-wise Habitat contrasts d.f. = 1. Significant effects are in bold.
449
450 **Table 3** Results from separate GLMMs on effect of Habitat (H) and Population (P) for each age/sex
451 category (AdM: adult male; SubM: subadult male; Bull; AdF: adult female; SubF: subadult female). If
452 the Habitat * Population interaction was significant, the main effects are not interpretable and,
453 instead, separate GLMMs for the effect of Population are presented for each habitat type (MW:
454 mixed woodland; AW: *Acacia* woodland; OP: open plain). Values in each cell are likelihood ratio tests
455 (p-values in italics) and, where Habitat was significant, t-tests (and p-values in italics) of pair-wise
456 contrasts between habitats. If the Habitat * Population interaction was not significant, main effects
457 of Habitat and Population are presented, and separate analyses for each Habitat are not applicable
458 (na). The degrees of freedom for Habitat and the Habitat * Population interaction was 2; for
459 Population and pair-wise Habitat contrasts d.f. = 1. Significant effects are in bold.

Figure 1 Location of the study sites in the Great Rift Valley region of Kenya. Base map provided by Google Maps 2018.

Figure 2 Frequency distributions of samples of group size for each study population.

Figure 3 Mean group size of giraffes in each study site, split by age/sex class (AdM = adult male, SubM = subadult male, Bull = big bull, AdF = adult female, SubF = subadult female, Juv = juvenile) and habitat type (AW = *Acacia* woodland, MW = mixed woodland, OP = open plain).

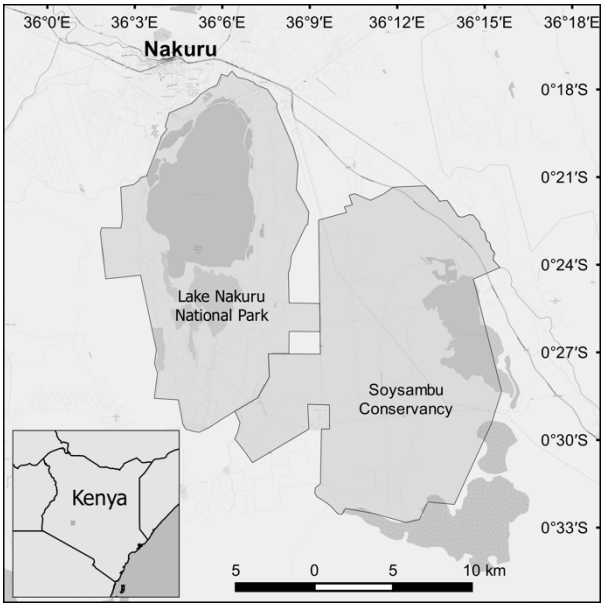
Figure 4 Mean group size of giraffes in each study site, following removal of juveniles. Abbreviations as in Fig. 3.

Figure 5 Mean group size of adult females, with and without calves, split by study site and habitat type. Abbreviations as in Fig. 3.

Author (Year)	Age/ Sex	HxP	Study site and region	Habitat	AW-MW	Subspecies	OP-MW	OP-AW	Length, season of study (if reported)	Population	Fenced?	SC - LNNP in MW	SC - LNNP in AW	SC - LNNP in OP	Total population size
Fennessy (2004)			Kunene Region, Northern Namib Desert, Namibia			*G. c. angolensis*			Long term data; 1981 to 2000		No				NR
Fennessy (2004)			Northern Namib Desert, Namibia - Khumib River (KR) - Hoarusib River (HR) - Hoanib River (HbR)			*G. c. angolensis*			Observed on a monthly basis over two-year period; 2002 and 2003		No				NR
Brand (2007)			Etosha National Park, Namibia			*G. c. angolensis*			May to December 2004, and March to December 2005		No				Estimated population 3550
Carter *et al.* (2013a)			Etosha National Park, Namibia			*G. c. angolensis*			May 2009 to June 2010		No				535 individuals in study area (3550 estimated in park)
Malyjurkova *et al.* (2014)			Bandia reserve, Senegal			*G. c. giraffa*			January to March 2013; dry season		Yes, 35km^2				28
Ciofolo (1995)			Niger, 100km south-east of Niamey			*G. c. peralta*			June to November 1990		No				50 – 100 individuals
Le Pendu *et al*. (2000)			Niger, 100km south-east of Niamey			*G. c. peralta*			October 1996 to December 1997		No				63
Shorrocks & Croft (2009)			Mpala Research Centre, Laikipia, Kenya			*G. c. reticulata*			Two four-week periods in March/April 2005 and March/April 2006		No				133 individuals used in study (total population NR)
VanderWaal *et al.* (2014)			Ol Pejeta Conservancy, Laikipia, Kenya			*G. c. reticulata*			One year; 2011		Yes, 365km^2				212
Bercovitch & Berry (2010)			Luangwa Valley, Zambia			*G. c. thornicrofti*			August 1971 to October 2005		No				600
Berry & Bercovitch (2015)[†]			Luangwa Valley, Zambia			*G. c. thornicrofti*			August 1971 to October 2005		No				600
Foster & Dagg (1972)			Nairobi National Park, Kenya			*G. c. tippelskirchi*			1965 to 1968		Yes, 117km^2				250
Leuthold (1979)			Tsavo East National Park, Kenya			*G. c. tippelskirchi*			August 1970 to October 1974		No				Unknown
van der Jeugd & Prins (2000)			Lake Manyara National Park, Tanzania			*G. c. tippelskirchi*			June to October 1991; dry season		Yes, 325km^2				101 individuals identified

AdM	3.00 *0.2229*	**16.01** ***0.0003***	**2.20** ***0.0278***	**4.01** ***<0.0001***	1.63 *0.1029*	0.04 *0.8468*	na	na	na
SubM	**6.33** ***0.0422***	na	na	na	na	na	3.25 *0.0712*	**11.03** ***0.0009***	0.01 *0.9254*
Bull	1.88 *0.3901*	**10.90** ***0.0043***	0.51 *0.6122*	**2.87** ***0.0042***	**3.27** ***0.0011***	**8.47** ***0.0036***	na	na	na
AdF	0.88 *0.6455*	**59.48** ***<0.0001***	**3.89** ***0.0001***	**8.18** ***<0.0001***	**3.28** ***0.0011***	**30.35** ***<0.0001***	na	na	na
SubF	**14.94** ***0.0006***	na	na	na	na	na	**6.36** ***0.0117***	**8.43** ***0.0037***	2.41 *0.1204*
Juv	3.95 *0.1384*	**18.48** ***<0.0001***	**0.64** *0.5210*	**4.74** ***<0.0001***	**2.49** ***0.0131***	**26.60** ***<0.0001***	na	na	na

Age/ Sex	HxP	Habitat	AW-MW	OP-MW	OP-AW	Population	SC - LNNP in MW	SC - LNNP in AW	SC - LNNP in OP
AdM	2.43 *0.29615*	**19.27** ***0.0001***	**2.588** ***0.0097***	**4.38** ***<0.0001***	1.62 *0.1064*	1.61 *0.2051*	na	na	na
SubM	**6.09** ***0.0477***	na	na	na	na	na	0.17 *0.6770*	**7.77** ***0.0053***	0.17 *0.6731*
Bull	2.06 *0.3571*	**10.98** ***0.0041***	0.23 *0.8204*	**3.18** ***0.0015***	**3.31** ***0.00098***	**4.12** ***0.0424***	na	na	na
AdF	5.38 *0.0678*	**67.92** *<0.0001*	**5.31** **<0.0001**	**8.62** **<0.0001**	**2.37** **0.0178**	1.55 *0.2136*	na	na	na
SubF	**21.20** **<0.0001**	na	na	na	na	na	**18.81** ***<0.0001***	**5.07** ***0.0243***	0.23 *0.6288*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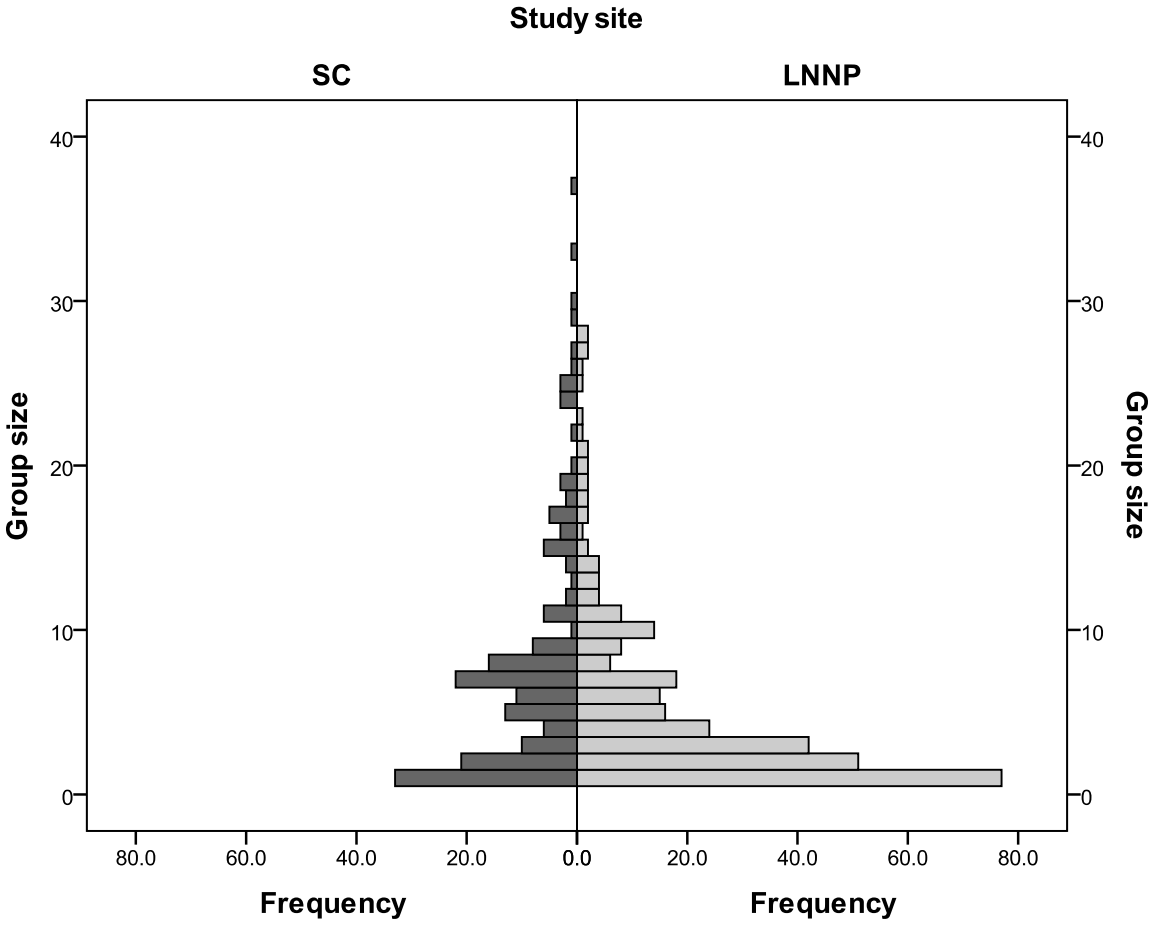
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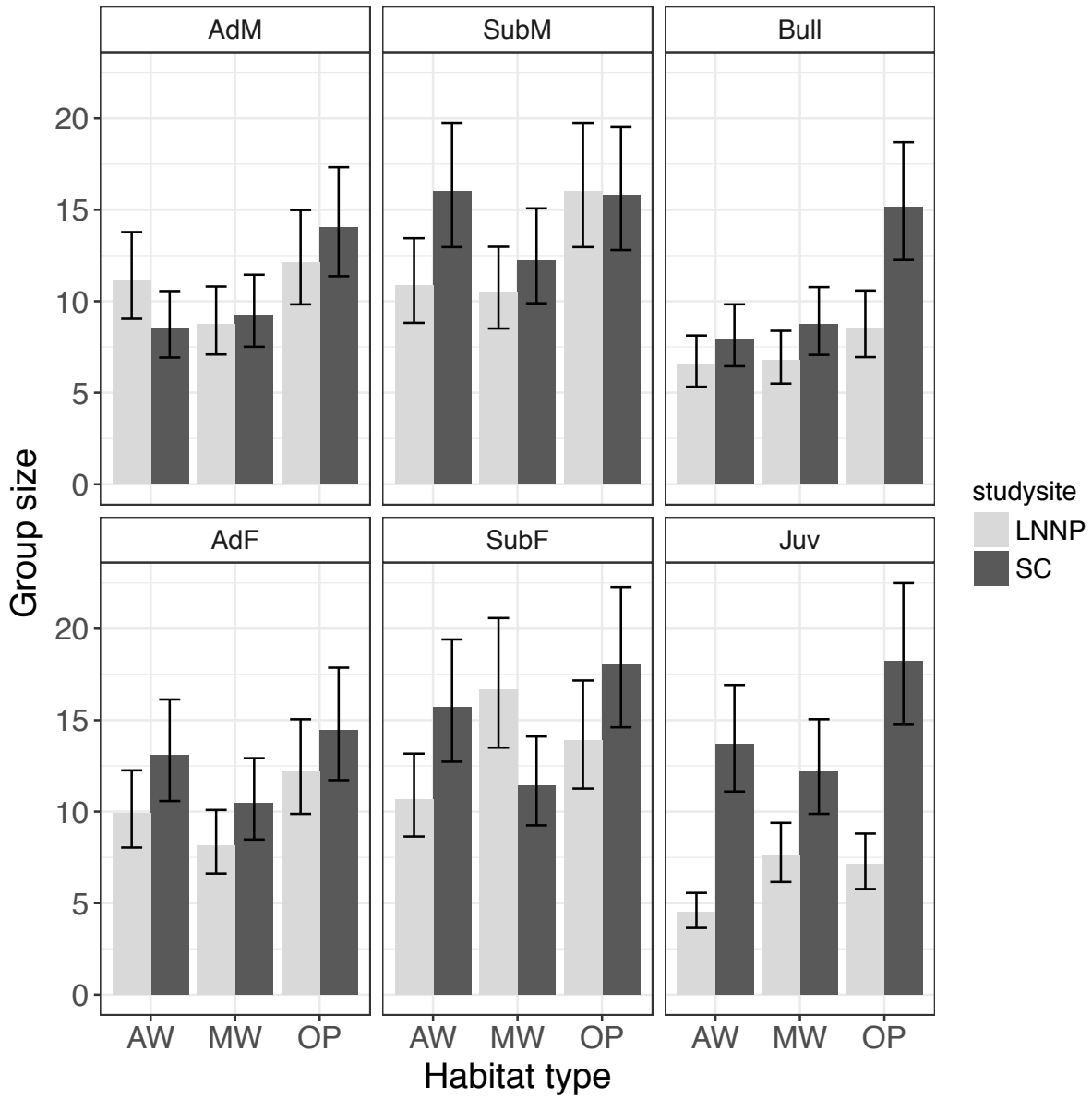
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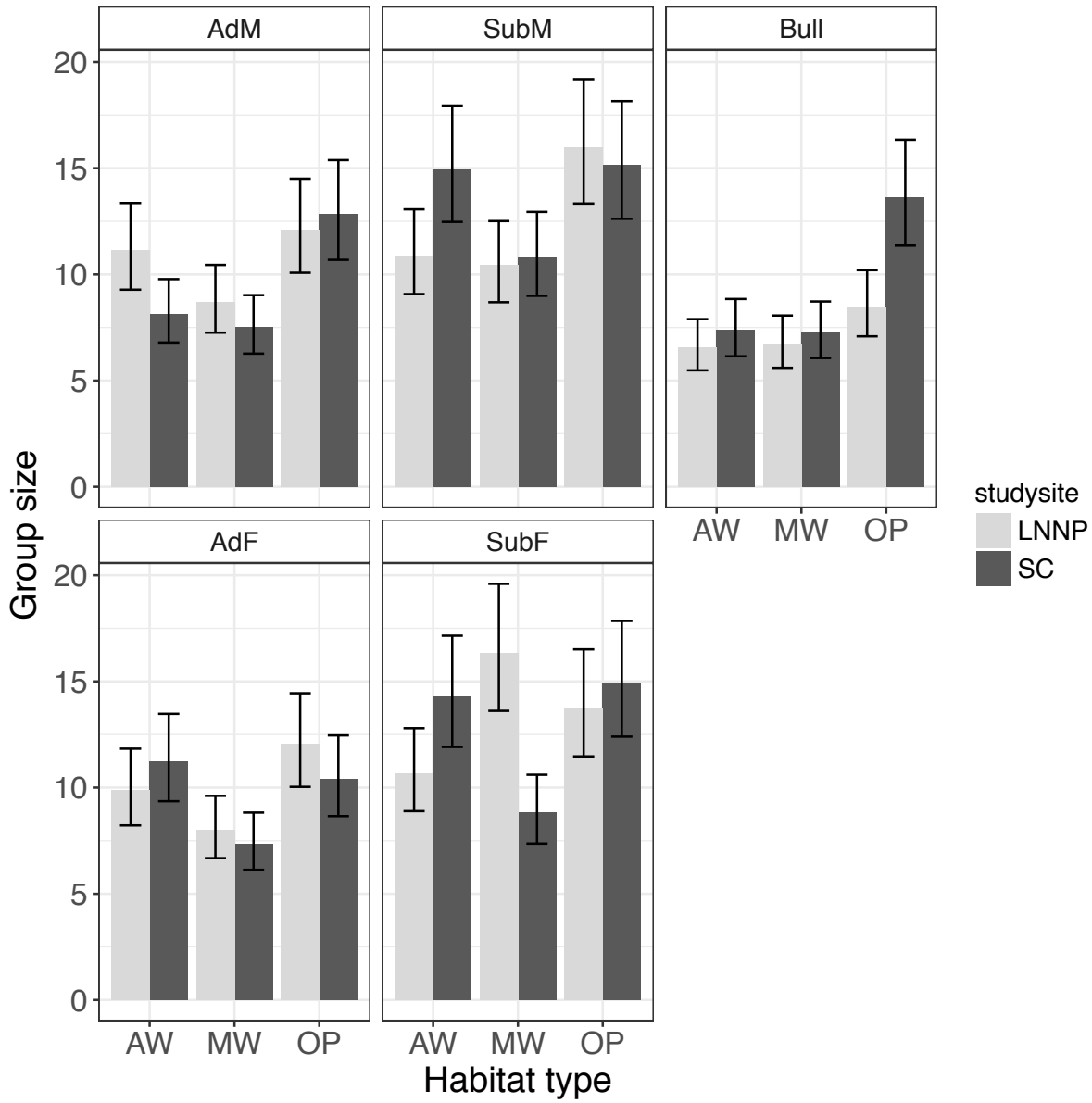
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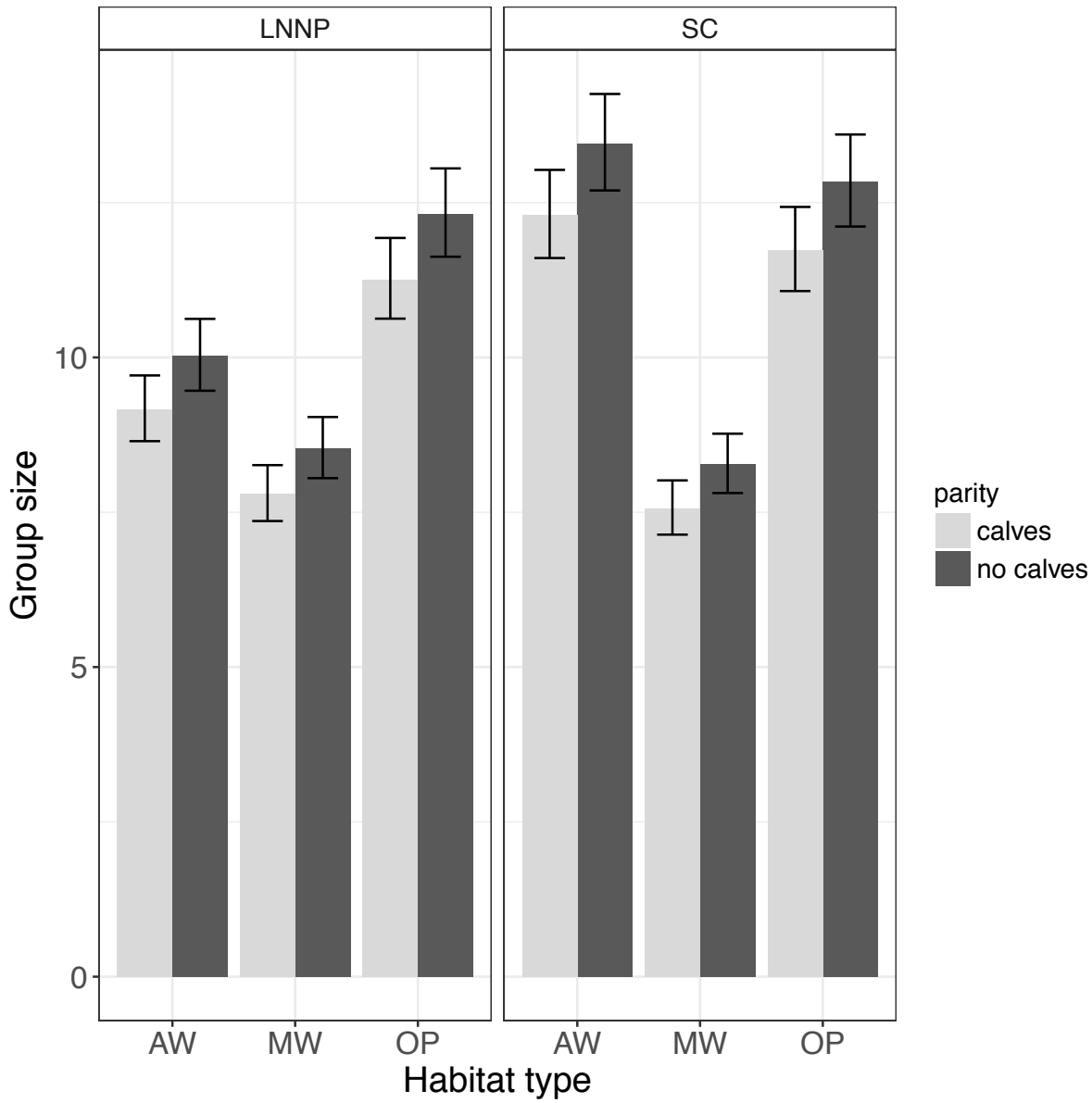
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parity
calves
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